# LIFE HISTORY AND DESCRIPTIONS OF IMMATURE STAGES OF *TRUPANEA ACTINOBOLA* (LOEW) (DIPTERA: TEPHRITIDAE) ON *ACAMPTOPAPPUS SPHAEROCEPHALUS* (HARVEY AND GRAY) GRAY (ASTERACEAE) IN SOUTHERN CALIFORNIA

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*Abstract.*—*Trupanea actinobola* (Loew) is an oligophagous, bivoltine fruit fly (Diptera: Tephritidae) infesting flower heads of *Acamptopappus, Amphipappus, Bailyea, Chloro-cantha, Gutierrezia, Psilostrophe,* and *Trichoptilium* spp. (Asteraceae) in southern California, and other plant genera throughout much of the United States. Two different-sized morphs are reported from California; the smaller one and subject of the present paper, is associated with *Acamptopappus, Amphipappus,* and *Gutierrezia* spp. in the subtribe Solidagininae of the tribe Astereae; the larger is associated with *Bailyea, Psilostrophe,* and *Trichoptilium* spp. in the subtribe Gaillardiinae of the tribe Helenieae. An uncommon, apparently intermediate-sized, presumably different biotype reared from flower heads of *C. spinosus,* a plant introduced into southern California from Mexico and Central America, may belong to a different, eastern United States' form of *T. actinobola* with different host affinities in the tribe Astereae. *Trupanea actinobola sensu lato* has now been reported from five tribes, eight subtribes, 14 genera, and 27 species of Asteraceae. The egg, first-third instars, and puparium obtained from *Acamptopappus sphaerocephalus* (Harvey and Gray) Gray are described and figured. The third instar larva bears a pair of elongated integumental petals dorsomediad of the mouth hooks, which have not been seen in the eight other California congeners described to date. The metathoracic lateral spiracular complex consists of a verruciform sensillum, and the abdominal lateral spiracular complex consists of a placoid-type sensillum; thus the lateral spiracular complex is the only morphological feature observed to differ among third instars of each of nine species of *Trupanea* studied to date. The life cycle of *T. actinobola* in southern California is of the aggregative type. Eggs are laid in closed, preblossom flower heads and inserted through the overlapping phyllaries. First instars feed on the ovules and florets, second instars on ovules, and third instars principally on the soft achenes. The receptacles of infested flower heads are not pitted by larval feeding. Four species of chalcidoid Hymenoptera were reared from individual puparia and mature flower heads bearing puparia of *T. actinobola* as solitary, primary, larval-pupal endoparasitoids: *Eurytoma veronia* Bugbee (Eurytomidae), *Halticoptera* sp. (Pteromalidae), *Mesopolobus* sp. (Pteromalidae), *Pteromalus* sp. (Pteromalidae).

*Key Words:* Insecta, *Trupanea,* Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, biotypes, host-plant range, parasitoids.

*Trupanea actinobola* (Loew) (Diptera: Tephritidae), as currently described, is a highly variable species belonging to one of the larger and more widespread genera of nonfrugivorous fruit flies in North America and California (Foote and Blanc 1963, Foote et al. 1993). Being of little or no economic importance, most species of *Trupanea* remained little known (Foote 1960, Foote et al. 1993) until detailed life histories of eight species from southern California were published (Cavender and Goeden 1982, Goeden 1987, 1988, Goeden et al. 1998, Goeden and Teerink 1997c, 1998, Headrick and Goeden 1991, Knio et al. 1996b), along with descriptions of the immature stages of seven of these species (Cavender and Goeden 1982, Goeden et al. 1998, Goeden and Teerink 1997c, 1998, Headrick and Goeden 1991, Knio et al. 1996a, Teerink and Goeden 1998). In this paper we describe the life history and immature stages of a ninth species, *T. actinobola.*

## MATERIALS AND METHODS

This study was based in large part on dissections of subsamples of flower heads of *A. sphaerocephalus* (Harvey and Gray) Gray infested by *T. actinobola* from samples collected during 1991–1997 in the low-elevation, Colorado (northern Sonoran) Desert and high-elevation, eastern Mojave Desert in southern California in the manner described by Goeden (1985, 1992). The principal study sites were both on *A. sphaerocephalus* at the margins of the Colorado Desert at the north end of Mason Valley, 650-m elevation, San Diego Co., and at Snow Creek, San Gorgonio Pass, at 370-m elevation, Riverside Co. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Twenty-eight eggs, 20 first-, 12 second-, and 12 third-instar larvae,

and 6 puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethlydisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a Philips XL30-FEG scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials were paired (n = 3) in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991, 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Knio et al. (1996a), Goeden et al. (1998), Goeden and Teerink (1997a, b, c, 1998), Teerink and Goeden (1998) and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *T. actinobola* and its parasitoids reside in the research collections
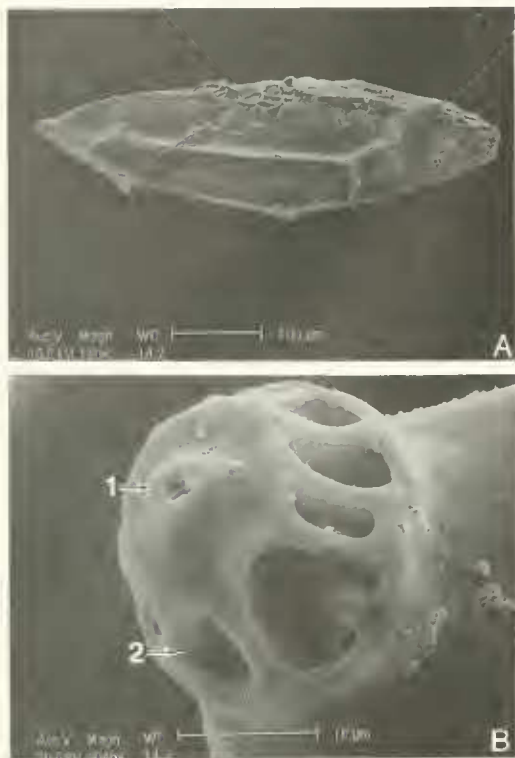
Fig. 1. Egg of *Trupanea actinobola:* (A) habitus, pedicel to left; (B) pedicel, 1 micropyle, 2—aeropyle.

of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae maintained by JAT.

## Results and Discussion

### Taxonomy

Adult.—*Trupanea actinobola* was first described by Loew (1873) as *Trypeta actinobola.* It was renamed *Urellia actinobola* by Coquillett (1899), and transferred to *Trupanea* by Benjamin (1934). A lectotype was designated by Foote (1960). Benjamin (1934), Foote (1960), Foote and Blanc (1963), and Foote et al. (1993) pictured the wing pattern of the female and male, which unlike some *Trupanea* spp., e.g. *T. bisetosa* (Coquillett), *T. imperfecta* (Coquillett), *T. jonesi* Curran, and *T. nigricornis* (Coquillett), is not sexually dimorphic. Benjamin (1934) also sketched the antenna of the

adult male, the male genitalia viewed from the posterior and side, the head of the adult female in frontal view, and the oviscape and fully extended ovipositor in dorsal view.

Size differences noted in adults reared from different subtribes of hosts are illustrated by measurements of thoracic dorsa listed in Table 1 and are fully discussed below relative to hosts of *T. actinobola.*

Immature stages.—The anterior spiracle, posterior spiracular area, and posterior spiracle of the puparium, and the dorsal aspect of the puparium itself were sketched by Benjamin (1934). The third instar of *T. actinobola* was described and the anterior spiracle, cephalopharyngeal skeleton, last abdominal segment, and posterior stigmatic chamber were drawn by Phillips (1946). Otherwise, the eggs, first and second instars, and puparium heretofore have not been described nor illustrated.

*Egg:* Thirty-one ova of *T. actinobola* dissected from a single, mature, field-collected female were white, opaque, smooth, elongate-ellipsoidal, 0.59 ± 0.004 (range, 0.56–0.64) mm long, 0.15 ± 0.002 (range, 0.14–0.18) mm wide, smoothly rounded at tapered basal end, pedicel 0.02 mm long (Fig. 1A), with raised micropyle (Fig. 1B-1) and a single row of aeropyles (Fig. 1B-2).

The egg of *T. actinobola* is longer than that of *T. californica* Malloch (Headrick and Goeden 1991), and shorter and narrower than other previously described *Trupanea* species (Goeden 1987, 1988, Goeden and Teerink 1997c, 1998, Goeden et al. 1998, Knio et al. 1996a). Pedicel and aeropyles are similar in size and shape to the other *Trupanea* species with the exception of *T. bisetosa,* which bears 1–2 rows of aeropyles (Knio et al. 1996a).

*Third instar:* White, barrel-shaped, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe the intersegmental lines (Fig. 2A); gnathocephalon conical (Fig. 2B), rugose pads dorsal and lateral to mouth lumen (Fig. 2B-1); dorsal sensory organ a dome-shaped papilla (Fig. 2B-2, 2C-1); sub-

dorsal sensilla laterad of dorsal sensory organ; anterior sensory lobe (Fig. 2B-3, 2C) with terminal sensory organ (Fig. 2C-2), pit sensory organ (Fig. 2C-3), lateral sensory organ (Fig. 2C-4), and supralateral sensory organ (Fig. 2C-5); stomal sense organ ventrolaterad of anterior sensory lobe (Fig. 2D-1); elongated integumental petals dorsomediad of mouth hook (Fig. 2D-2); mouth hook tridentate (Fig. 2D-3); median oral lobe laterally flattened, tapering anteriorly (Fig. 2D-4); six pit sensilla circumscribe gnathocephalon posteriorad of rugose pads (Fig. 2B-4); prothorax with minute acanthae dorsally and ventrally (Fig. 2E-1); rugose pads circumscribe prothorax anteriorly (Fig. 2E-2); single row of verruciform sensilla circumscribe prothorax posteriorad of rugose pads (Fig. 2E-3); stelex sensillum located dorsomedially (Fig. 2E-4); anterior thoracic spiracle on posterior margin of prothorax bears 3–4 rounded papillae (Fig. 2E-5); metathoracic lateral spiracular complex consists of a spiracle (Fig. 2F-1) and a verruciform sensillum (Fig. 2F-2); abdominal lateral spiracular complex consists of a spiracle (Fig. 2G-1) and a placoid-type sensillum (Fig. 2G-2); caudal segment with minute acanthae dorsally and ventrally; stelex sensilla circumscribe caudal segment in 2-dorsal, 4-ventral arrangement (Fig. 2H-1); pair of verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 2H-2); posterior spiracular plates bear three ovoid rima, ca. 0.028mm in length (Fig. 2H-3), and four interspiracular processes, each with 2–4 branches, longest measuring 0.012 mm (Fig. 2H-4); intermediate sensory complex consists of a medusoid sensillum and a stelex sensillum (Fig. 2H-5).

The third instar larva of *Trupanea actinobola* is similar in general habitus to *T. bisetosa, T. californica, T. jonesi, T. nigricornis* and *T. signata* (Goeden and Teerink 1997c; Goeden et al. 1998; Headrick and Goeden 1991; Knio et al. 1996a). *Trupanea pseudovicina* Hering differs in general habitus in being elongate-cylindrical (Goeden and Teerink 1998), and *T. conjuncta* (Adams)

differs in having a punctate integument (Teerink and Goeden 1998). The gnathocephalon is very similar in sensory structures to all other *Trupanea* species previously described, however *T. actinobola* bears an elongated pair of integumental petals dorsomediad of the mouth hooks, which have not been seen in other *Trupanea* species previously studied (Goeden and Teerink 1997c, 1998, Goeden et al. 1998, Headrick and Goeden 1991, Knio et al. 1996a, Teerink and Goeden 1998). The rugose pads are smooth, not serrated as in *T. jonesi, T. nigricornis, T. pseudovicina,* and *T. signata* (Goeden and Teerink 1997c, 1998, Goeden et al. 1998, Knio et al. 1996a). Minute acanthae on the prothorax do not completely circumscribe the segment as in the other *Trupanea* species (Goeden and Teerink 1997c, 1998, Goeden et al. 1998, Headrick and Goeden 1991, Knio et al. 1996a, Teerink and Goeden 1998). The lateral spiracular complex is unique among the *Trupanea* species previously studied. *Trupanea actinobola* differs from *T. jonesi* in lacking the stelex sensillum in the metathorax (Goeden et al. 1998), and from *T. signata* in lacking a verruciform sensillum in the abdominal segments (Goeden and Teerink 1997c). The caudal segment of *T. actinobola* bears fewer minute acanthae than other *Trupanea* species studied, and these acanthae do not completely circumscribe the posterior spiracular plates. The rimae are shorter (0.028 mm) than rimae in other Trupanea species (0.034–0.04 mm) (Goeden and Teerink 1997c, 1998, Goeden et al. 1998, Headrick and Goeden 1991, Knio et al. 1996a, Teerink and Goeden 1998).

*Second instar.* White, barrel-shaped, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines (Fig. 3A); gnathocephalon conical; rugose pads dorsal and lateral of mouth lumen (Fig. 3B-1); dorsal sensory organ a dome-shaped papilla (Fig. 3B-2, 3C-1); subdorsal sensilla laterad of dorsal sensory organ (Fig. 3C-2); anterior sensory lobe bears the terminal sensory organ (Fig. 3C-3), pit sen-
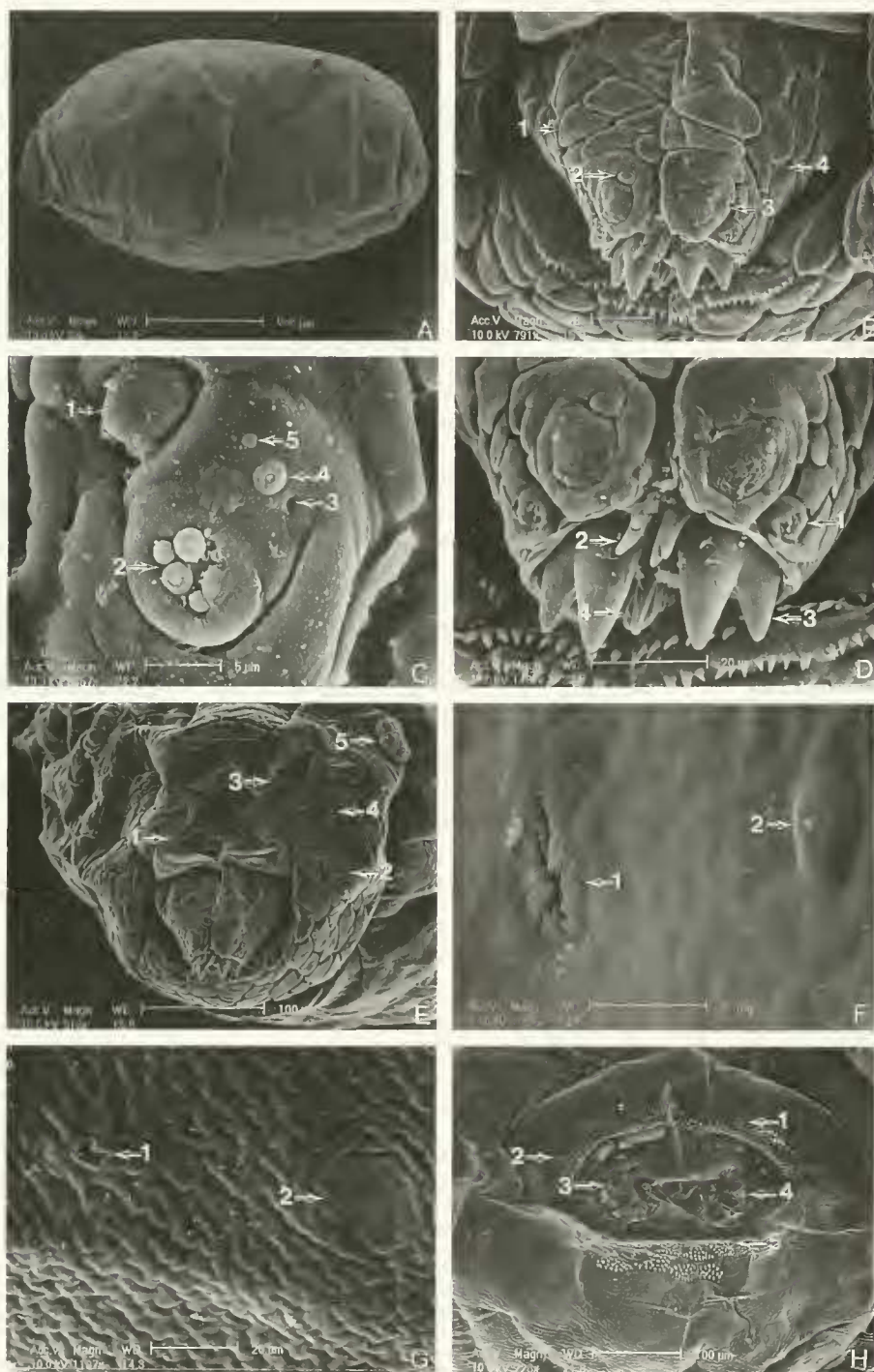
Fig. 2.   Third instar of *Trupanea actinobola:* (A) habitus, anterior end to left; (B) gnathocephalon, anterior view, 1, rugose pads, 2, dorsal sensory organ, 3, anterior sensory lobe, 4, pit sensillum; (C) anterior sensory lobe, 1, dorsal sensory organ, 2, terminal sensory organ, 3, pit sensory organ, 4, lateral sensory organ, 5, supralateral sensory organ; (D) gnathocephalon, anterior view, 1, stomal sense organ, 2, integumental petals, 3,

sory organ (Fig. 3C-4), lateral sensory organ (Fig. 3C-5), and supralateral sensory organ (Fig. 3C-6); stomal sense organ ventrolateral of anterior sensory lobe (Fig. 3B-3); mouth hooks bidentate (Fig. 3B-4, 3D-1); median oral lobe laterally flattened (Fig. 3B-5, 3D-2); minute acanthae dorsally and ventrally on anterior margin of prothorax (Fig. 3D-3); rugose pads (Fig. 3D-4) and verruciform sensilla circumscribe prothorax; anterior thoracic spiracles bear 3–4 rounded papillae (Fig. 3E); metathoracic lateral spiracular complex consists of a spiracle and a verruciform sensillum; abdominal lateral spiracular complex not seen; posterior spiracular plates bear three ovoid rimae, ca. 0.014 mm in length (Fig. 3F-1), and four interspiracular processes, each with 1–3 branches, longest measuring 0.01 mm (Fig. 3F-2); intermediate sensory complex consists of a medusoid sensillum (Fig. 3F-3) and a stelex sensillum (Fig. 3F-4).

The second instar is very similar to the third instar in general habitus and sensory structures, but differs in that the mouth hooks are bidentate and the integumental petals are not elongated. The rugose pads and minute acanthae on the prothorax are weakly defined. Rugose pads are lacking in the second instars of *T. pseudovicina* (Goeden and Teerink 1998), and *T. conjuncta* (Teerink and Goeden 1998). The interspiracular processes have fewer branches than the third instar.

*First instar:* White, elongate-cylindrical, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines (Fig. 4A); gnathocephalon smooth, lacking rugose pads (Fig. 4C); dorsal sensory organ a dome-shaped papilla (Fig. 4B-1); subdorsal sensilla laterad of dorsal sensory organ (Fig. 4B-2); anterior sensory

lobe (Fig. 4C-1) bears the terminal sensory organ (Fig. 4B-3), pit sensory organ (Fig. 4B-4), lateral sensory organ (Fig. 4B-5), and supralateral sensory organ (Fig. 4B-6); stomal sense organ ventrad of anterior sensory lobe (Fig. 4C-2); integumental petals dorsad of mouth hooks (Fig. 4C-3); mouth hooks bidentate (Fig. 4C-4); median oral lobe laterally flattened (Fig. 4C-5); labial lobe attached to median oral lobe, with two pore sensilla (Fig. 4C-6); minute acanthae on ventral margin of prothorax (Fig. 4C-7); prothorax smooth lacking rugose pads; anterior thoracic spiracle not present; lateral spiracular complex not seen; stelex sensilla circumscribe caudal segment in 2-dorsal, 4-ventral arrangement (Fig. 4D-1); posterior spiracular plates bear two ovoid rimae, ca. 0.006 mm in length (Fig. 4D-2), and four interspiracular processes each with 1–3 branches, longest measuring 0.006 mm (Fig. 4D-3); intermediate sensory complex consists of a medusoid sensillum (Fig. 4D-4), and a stelex sensillum (Fig. 4D-5).

The first instar differs from the second instar in lacking rugose pads on the gnathocephalon and prothorax. There are fewer minute acanthae ventrally on the anterior margin of the prothorax and circumscribing the intersegmental lines. The integumental petals in the first instar consist of a single pair of enlarged petals; the later instars have more, but smaller petals with the exception of the single pair of elongated petals seen in the third instar. The dorsal sensory organ, subdorsal sensilla, and anterior sensory lobe are very similar in the later instars, but the stomal sense organ is greatly reduced. The interspiracular processes are not greatly reduced as in *T. jonesi* (Goeden et al. 1998).

*Puparium:* Black, elongate-cylindrical, minute acanthae circumscribe intersegmen-

mouth hooks, 4, median oral lobe; (E) anterior view, 1, minute acanthae, 2, rugose pads, 3, verruciform sensillum, 4, stelex sensillum, 5, anterior thoracic spiracle; (F) metathoracic lateral spiracular complex, 1, spiracle, 2, verruciform sensillum; (G) abdominal lateral spiracular complex, 1, spiracle, 2, placoid-type sensillum; (H) caudal segment, 1, stelex sensillum, 2, verruciform sensillum, 3, rima, 4, interspiracular process, 5, intermediate sensory complex.
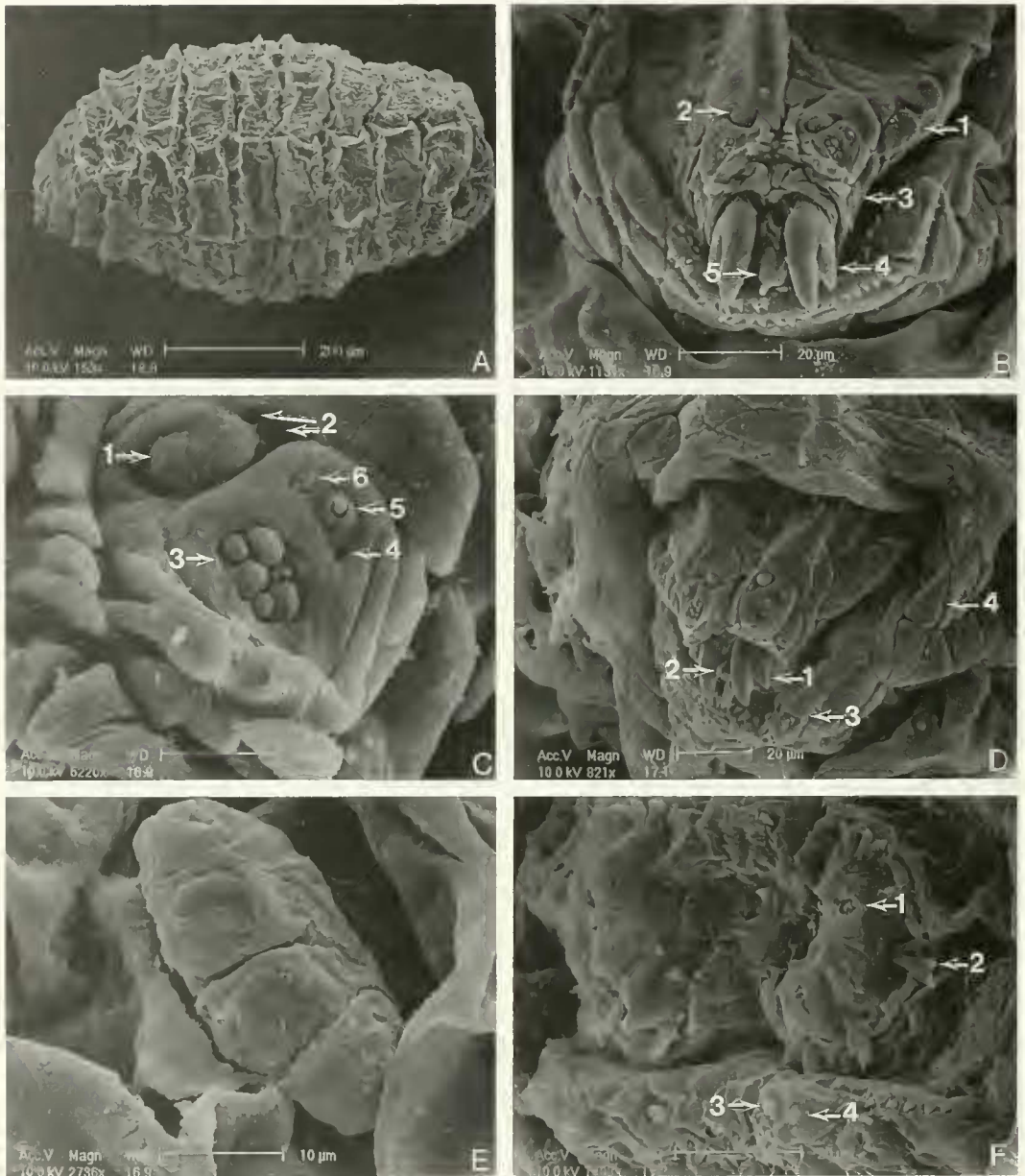
Fig. 3.   Second instar of *Trupanea actinobola:* (A) habitus, anterior to left; (B) gnathocephalon, anterior view, 1, rugose pads, 2, dorsal sensory organ, 3, stomal sense organ, 4, mouth hooks, 5, median oral lobe; (C) anterior sensory lobe, 1, dorsal sensory organ, 2, subdorsal sensilla, 3, terminal sensory organ, 4, pit sensory organ, 5, lateral sensory organ, 6, supralateral sensory organ; (D) anterior view, 1, mouth hooks, 2, median oral lobe, 3, minute acanthae, 4, rugose pads; (E) anterior thoracic spiracle; (F) caudal segment, 1, rima, 2, interspiracular process, 3, intermediate sensory complex, medusoid sensillum, 4, intermediate sensory complex, stelex sensillum.
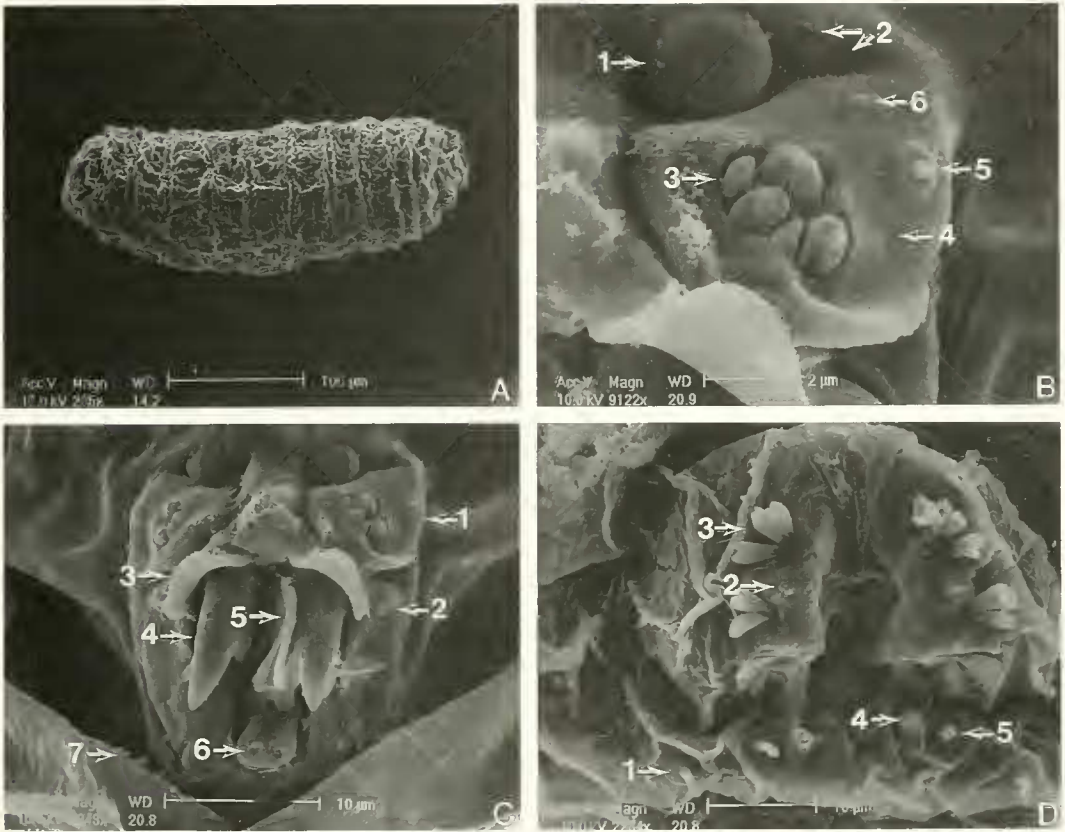
Fig. 4. First instar of *Trupanea actinobola:* (A) habitus, anterior to right; (B) anterior sensory lobe, 1—dorsal sensory organ, 2—subdorsal sensilla, 3—terminal sensory organ, 4—pit sensory organ, 5—lateral sensory organ, 6—supralateral sensory organ; (C) gnathocephalon, anterior view, 1—anterior sensory lobe, 2—stomal sense organ, 3—integumental petal, 4—mouth hooks, 5—medial oral lobe, 6—labial lobe pore sensillum, 7—minute acanthae; (D) caudal segment, 1—stelex sensillum, 2—rima, 3—interspiracular process, 4—intermediate sensory complex, medusoid sensillum, 5—intermediate sensory complex, stelex sensillum.

tal lines (Fig. 5A); anterior end bears the invagination scar (Fig. 5B-1), and anterior thoracic spiracle (Fig. 5B-2); caudal segment circumscribed by minute acanthae (Fig. 5C-1), stelex sensilla in 2-dorsal, 4-ventral arrangement (Fig. 5C-2); two verruciform sensilla dorsolaterad of posterior spiracular plates (Fig. 5C-3); posterior spiracular plates bear three ovoid rimae (Fig. 5C-4), and four interspiracular processes, each with 2–4 branches (Fig. 5C-5); intermediate sensory complex consists of a medusoid sensillum and a stelex sensillum (Fig. 5C-6). Forty-nine puparia averaged 1.98 ± 0.02 (range, 1.72–2.37) mm in

length; 0.93 ± 0.01 (range, 0.72–1.13) mm in width.

Puparia of *T. actinobola* are similar in size to *T. californica* (Headrick and Goeden 1991), but smaller than the other *Trupanea* species previously studied (Goeden 1987, 1988, Goeden and Teerink 1997c, 1998, Goeden et al. 1998, Knio et al. 1996a).

## DISTRIBUTION AND HOSTS

The distribution of *T. actinobola* in North America north of Mexico as mapped by Foote et al. (1993) included two or more locations each in Alabama, Arizona, California, Colorado, Florida, Georgia, Idaho,

Indiana, Iowa, Kansas, Michigan, Montana, Nevada, New Mexico, New York, South Carolina, Texas, Utah, and Wyoming; single locations each in Delaware, Indiana, Kentucky, Louisiana, Mississippi, Nebraska, Oklahoma, and Tennessee, and Ontario and Saskatchewan, Canada; and general state records only for South Dakota and Virginia.

Benjamin (1934) reported *T. actinobola* as reared from *Aster adnatus* Nuttall, *A. carolinianus* Walter, *A. simmondsii* Small, *Balduina* (as *Actinospermum*) *angustifolia* (Pursh) B. L. Robinson, *Coreopsis* sp., and *Hieracium* sp. Stegmaier (1968) noted that Benjamin (1934) also listed *Erigeron quercifolius* Lange, *E. vernus* (L.) Torrey and Gray, and *Solidago* sp. as hosts, but did not report rearing the flies from these plant species. Stegmaier (1968) studied *T. actinobola* on *E. strigosus* Muhlenberg in Florida, and reported that Phillips (1946) had reported "*E. sondbergiana* (author unknown)" as another larval host from New York. Foote (1960) added *Solidago chapmanii* Torrey and Gray and *S. serotina* Aiton as additional hosts of reared adults of *T. actinobola*. Finally, Wasbauer (1972) added *Hieracium paniculatum* L., *Pyrrhopappus* (as *Sitilias*) *caroliniana* (Walter) deCandolle, *Solidago caesia* L. [cited in error from, but not in, Stegmaier (1968)], and *S. stricta* Aiton. Of these purported hosts only *E. strigosus* occurs in California as a scattered adventive weed (Hickman 1993). We have not sampled flower heads of *E. strigosus*, but *T. actinobola* has not been reared from a total of at least 75 1-liter samples of mature flower heads from other 12 species of *Erigeron* (Goeden 1985, 1992, unpublished data). Similarly, *T. actinobola* has neither been reared from a total of 60 samples of flower heads of 14 *Aster* spp., from 20 samples of flower heads of six *Coreopsis* spp., nor from 40 samples of flower heads from six other species of *Solidago* from California collected to date (Goeden 1985, 1992, unpublished data; see corrections below). Therefore, the above host records compiled in Wasbauer (1972) remain unconfirmed for *Aster, Erigeron, Coreopsis,* or *Solidago* spp. in California, which suggests that they instead refer to one or more, different, eastern-U.S., host-based biotype(s) of *T. actinobola,* or to another, as yet undistinguished, separate species of *Trupanea.*

To further explore the latter possibilities, the senior author reexamined all reared voucher specimens of *T. actinobola* reported by Goeden (1985, 1992) using the latest version of separate keys for each sex of *Trupanea* in Foote et al. (1993), and found several, mostly single, reared specimens, he misidentified since 1980. During this period, the principal characters separating this variable tephritid species from its close congeners were better defined in keys (Foote and Blanc 1963, Foote et al. 1993) and became better known and appreciated as a series of reared specimens of most California species also were acquired for comparison by RDG. Accordingly, it was determined that rearing records for *T. actinobola* from flower heads of the following hosts in Goeden (1985, 1992) were erroneous and should be reassigned to *T. wheeleri: Achillea millefolium* L., *Aster occidentalis* (Nuttall) Torrey and Gray, *Brickellia oblongifolia* Nuttall, *Ericameria* (as *Haplopappus*) *cooperi* (Gray) Hall, *Erigeron foliosus* Nuttall, *Eriophyllum ambiguum* (Gray) Gray, *Hazardia* (as *Haplopappus*) *squarrosus* Hooker and Arnott, *Lepidospartum squamatum* (Gray) Gray, *Orochaenactis thysanocarpha* (Gray) Coville, *Porophyllum gracile* Bentham, and *Solidago confinis* Gray. Of these plant species, *B. oblongifolia* and *H. squarrosus* already were reported as hosts of *T. wheeleri* (Goeden 1985, 1992). Similarly, the rearing record from *Ericameria* (as *Haplopappus*) *bloomeri* Gray for *T. actinobola* in Goeden (1992) should instead be reassigned as new for *T. femoralis;* whereas, the rearing record from *Heterotheca grandiflora* Nuttall for *T. actinobola* in Goeden (1985) should be reassigned as new for *T. radifera.* Host records for *T. ac-*

Fig. 5. Puparium of *Trupanea actinobola:* (A) habitus, anterior to right; (B) anterior end, t—invagination scar, 2—anterior thoracic spiracle; (C) caudal end, 1—minute acanthae, 2—stelex sensillum, 3—verruciform sensillum, 4—rimae, 5—interspiracular process, 6—intermediate sensory complex.

*tinobola* from *Trixis californica* Kellogg in Goeden and Ricker (1989) should be reassigned wholly or in large part to *T. arizonensis* Malloch, as suggested by Goeden

(1992), who reported it as the only known host plant of the latter species. Finally, *Dyssodia* (= *Thymophylla*) *pentachaeta* (deCandolle) Robinson should be reassigned from *T. actinobola* to *Trupanea vicina* (Wulp), which previously was reported as reared from another species of *Dyssodia* (Goeden 1985). Consequently, instead of the nine tribes, 22 genera, and 38 species reported by Goeden (1992), *T. actinobola*, as updated and corrected to date, has now been reported from five tribes, eight subtribes, 14 genera and 27 species of Asteraceae (Wasbauer 1972, Goeden 1985, 1992, Hickman 1993, Bremer 1994). The five tribes are the Astereae, Heleniae, Gnaphalieae, Lactuceae, and Mutiseae; the eight subtribes are the Asterinae, Coreopsidinae, Gailardiinae, Gnaphaliinae, Hieraciinae, Microseridinae, Nassauviinae, and Solidagininae (Bremer 1994).

However, ignoring the above-mentioned, mostly out-of-State, host records compiled by Wasbauer (1972), as well as those noted above as previously assigned in error by RDG to *T. actinobola* (Goeden 1985, 1992), now leads us to conclude that this tephritid in California is less widely oligophagous than previously surmized. We now believe that among host plants reported to date from California, a smaller form or biotype of *T. actinobola* (Table 1) is confined to *Acamptopappus sphaerocephalus*, *A. shockleyi* Gray, *Amphipappus fremontii* Torrey and Gray, *Gutierrezia californicum* (deCandolle) Torrey and Gray, *G. microcephala* (deCandolle) Gray, and *G. sarothrae* (Pursh) Britton and Rusby (Goeden 1985, 1992), all found in the subtribe Solidagininae of the Astereae (Bremer 1994). In addition, a larger form or biotype (Table 1) that also keys to *T. actinobola* in Foote et al. (1993) has been recovered from flower heads of *Bailyea multiradiata* Harvey and Gray, *B. pleniradiata* Harvey and Gray, *Psilostrophe cooperi* (A. Gray) E. Greene, and *Trichoptilium incisum* (Gray) Gray, all of which belong to the subtribe Gaillardiinae of the tribe Helenieae. *Psilostrophe*

Table 1. Mean lengths (mm) of thoracic dorsa of three presumed biotypes of *T. actinobola* individually reared from flower heads of different host genera in southern California.

| Host-plant | Sex | Mean Length[a] ± SE (Range) | N |
|---|---|---|---|
| *Acamptopappus sphaerocephalus* | ♂ | 0.84[b] ± 0.02 (0.77–1.00) | 12 |
| | ♀ | 0.91[b] ± 0.02 (0.86–0.99) | 12 |
| *A. shockleyi* | ♂ | 0.76[b] ± 0.01 (0.66–0.83) | 12 |
| | ♀ | 0.82[b] ± 0.02 (0.76–0.93) | 12 |
| *Bailyea multiradiata* | ♂ | 1.32[c] ± 0.01 (1.26–1.39) | 12 |
| | ♀ | 1.37[c] ± 0.02 (1.22–1.47) | 12 |
| *B. pleniradiata* | ♂ | 1.16[c] ± 0.02 (1.03–1.28) | 12 |
| | ♀ | 1.21[c] ± 0.03 (0.97–1.31) | 12 |
| *Chloracantha spinosus* | ♂ | 1.11 ± 0.02 (1.08–1.13) | 3 |
| | ♀ | 1.08 ± 0.03 (1.02–1.17) | 4 |

[a] Means followed by a different letter were significantly different at 0.05 as determined by Tukey's test.

*cooperi* is a newly reported host for *T. actinobola*, 2 ♂ and 5 ♀ having been reared from flower heads collected at Mercury Mountain, San Bernardino Co., on 7.iv.1992. Unfortunately, we have little-studied this larger form to date, which conceivably may be a separate species.

An analysis of variance followed by Tukey's test for differences in means showed that adults reared from *Acamptopappus* spp. were significantly smaller than adults reared from *Bailyea* spp. (Table 1). Other smaller differences were also identified among adults reared from each host plant species, and between sexes, but the major difference was between those reared from the two genera. In addition, seven specimens of intermediate size (3 ♂ and 4 ♀) have been reared from *Chloracantha* (= *Aster*) *spinosus* L. (Table 1), a weedy plant species introduced to California from Mexico and Central America, which may represent a third biotype like that reported from *Aster* spp. in the eastern U.S., and belonging to the subtribe Asterinae of the tribe Astereae. Again, were it not for the voucher specimens and series of reared specimens of *Trupanea* spp. available to us for study, we could not have determined the host ranges of these separate size-morphs of *T. actinobola* in California with this degree of certitude (Table 1). *Trupanea actinobola sensu lato* attacks additional host plants and genera outside of California, as the records in

Wasbauer (1972) indicate, but whether as host-based biotype, or as yet undistinguished, additional, separate species, remains a question for future studies by others outside of California to answer.

## BIOLOGY

Egg.—In 31 closed, preblossom, immature flower heads of *A. sphaerocephalus* averaging 2.1 ± 0.1 (range, 0.9–3.36) mm in diam (Fig. 6A), a total of 56 eggs and an average of 1.8 ± 0.2 (range, 1–5) eggs were inserted pedicel-last, mostly through the phyllaries. Most were deposited parallel to the receptacle and between the florets on the periphery of the flower head (Fig. 6B). In only five flower heads (16%) were a few eggs among those deposited placed at acute angles to the long axis of a head or perpendicular to the receptacle (Fig. 6B). Only two of the 56 eggs (3.6%) were inserted partially into separate florets. Most eggs were oviposited singly (Fig. 6B) or side-by-side in pairs by one or more females. Stegmaier (1968) reported oviposition of 1–12 eggs by females preferentially in the centers of unopened, immature flower heads of *E. strigosus* in Florida.

Larva.—Upon eclosion, first instars tunneled into and fed mainly in floral tubes and ovules of preblossom flower heads. An average of 1.2 ± 0.1 (range, 1–2) first instars was found feeding within 25 closed, preblossom flower heads. The receptacles of
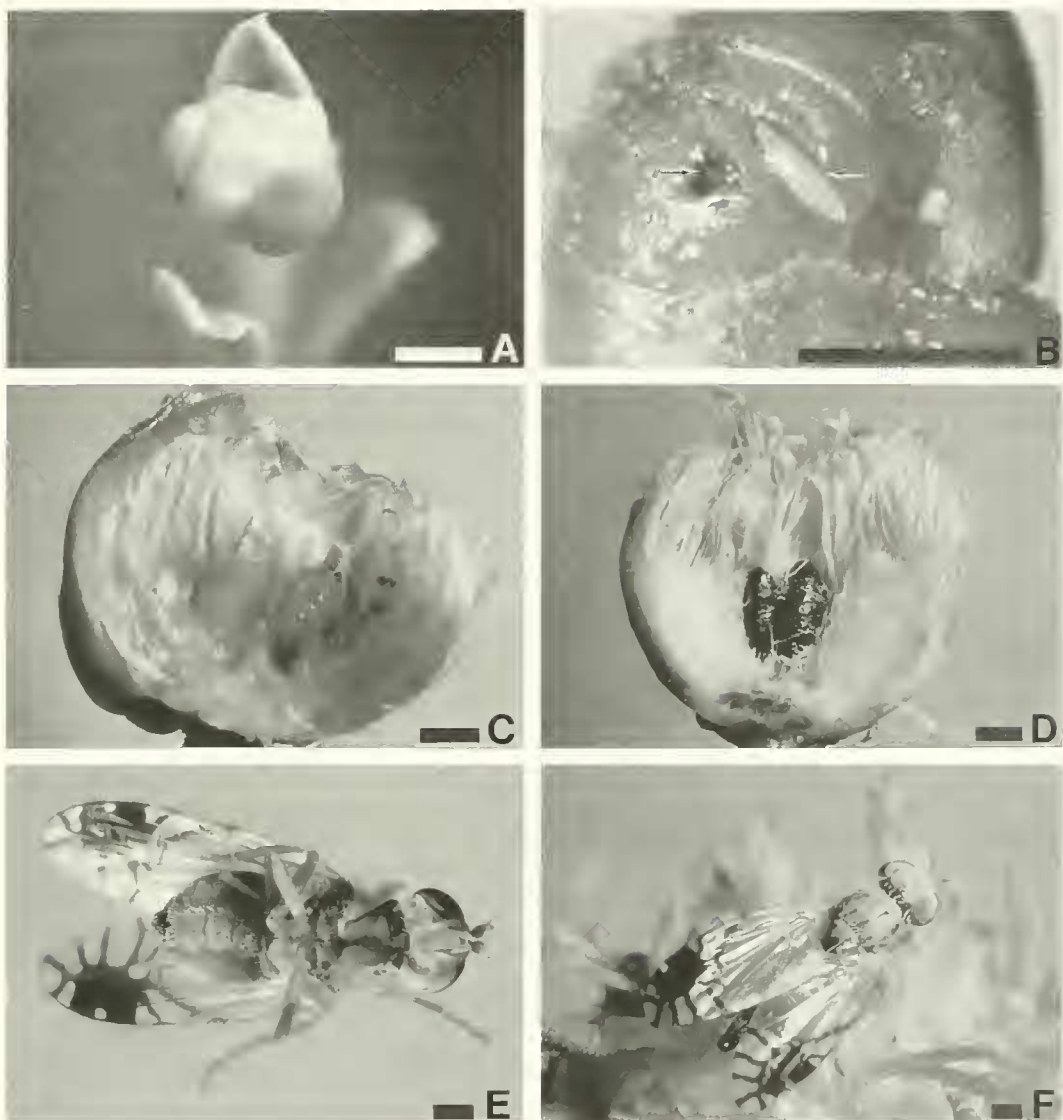
Fig. 6.   Life stages of *Trupanea actinobola* in or on *Acamptopappus sphaerocephalus:* (A) immature, pre-blossom flower head preferred for oviposition; (B) two eggs (arrows), one inserted parallel to, and one perpendicular to, and between florets in closed, preblossom flower head; (C) early third instar tunneling in soft achene; (D) two puparia in center of open flower head; (E) ventral view of adult male displaying abdominal pleural distension; (F) adult female on flower head. Lines = 1 mm.

these heads averaged 2.5 ± 0.2 (range, 1.5–5.1) mm in diameter. These heads contained an average of 18 ± 1.3 (range, 14–22) florets, of which an average of 2.2 ± 0.3 (range, 0–6) ovules/floral tubes, or 17% (range, 9–36%), were damaged. No receptacle within these 25 infested flower heads was pitted by first-instar feeding.

Second instars fed mainly on ovules and tunnelled parallel to, but well above, the receptacles of preblossom flower heads. Receptacles of 16 unopen flower heads containing second instars averaged 2.7 ± 0.2 (range, 1.7–4.6) mm in diameter. These flower heads contained an average of 1.1 ± 0.1 (range, 1–2) second instars that had de-

stroyed an average of 2.9 ± 0.4 (range, 1–8) ovules, or 15% (range, 4.2–4.4%) of an average total of 22 ± 1.0 (range, 18–26) ovules per head. Stegmaier (1968) also reported that larvae fed preferentially on ovules and soft achenes.

Third instars fed on soft achenes at the centers, and less commonly towards the margins, of open or postblossom heads (Fig. 6C). Heavily attacked preblossom flower heads never opened. In 14 flower heads averaging 2.9 ± 0.2 (range, 2.2–4.9) mm in diameter and containing an average of 1.4 ± 0.1 (range, 1–2) third instars, an average of 2.9 ± 0.4 (range 1–6) ovules/ soft achenes were damaged, or 15% (range, 4–33%). Most third instars fed with their long axes oriented perpendicular to, and mouthparts directed towards, the receptacles, within the upper parts of the soft achenes, and well above the receptacles. Consequently, no receptacles were pitted in the 14 flower heads that contained third instars (Fig. 6C). Upon completing feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and pupariated.

Pupa.—Flower heads containing puparia (Fig. 6D) reflected the greatest amount of damage that the seed-feeding larvae of *T. actinobola* caused within flower heads sampled. The receptacles of 49 infested, blossom and postblossom flower heads containing puparia averaged 3.7 ± 0.1 (range, 2.2–5.3) mm in diameter and bore an average total of 23.6 ± 1.0 (12–48) soft achenes, of which an average of only 2.4 ± 0.2 (range, 1–8) soft achenes or 11% (range, 4–40%) were damaged. Again, no receptacles were pitted. Stegmaier (1968) reported that one larva destroyed 32 achenes, or about 10% of those in a flower head of *E. strigosus*.

Our sampled heads of *A. sphaerocephalus* contained an average of 1.3 ± 0.1 (range, 1–5) puparia; whereas, Stegmaier (1968) reported from 2–12 puparia in flower heads of *E. strigosus*. Puparia of *T. actinobola* were found alongside of the phyllaries at the margins in 13 flower heads; the

remaining heads contained puparia at their centers (Fig. 6D). All puparia had their anterior ends facing away from the receptacles, and their long axes were perpendicular to the receptacles (Fig. 6D).

Adult.—Adults emerged from mature flower heads, and were long-lived under insectary conditions, as 17 unmated males (Fig. 6E) averaged 104 ± 9 (range, 41–150) days, and seven virgin females (Fig. 6F) averaged 128 ± 15 (range, 65–171) days. Like *T. pseudovicina* (Goeden and Teerink 1998), these flies are among the longer average and maximum adult longevities that we have recorded for native species of nonfrugivorous Tephritidae from southern California. Such lengthy longevities are consistent with the aggregative type of life cycle ascribed below to this tephritid.

The premating and mating behaviors of *T. actinobola* were briefly studied in the field, and unlike most congeners that we have studied, a high proportion, i.e. two of three pairs, of adults mated once each in the petri dish arenas found to be so useful with many other noncongeneric, nonfrugivorous species (Headrick and Goeden 1994).

*Wing displays*: Both sexes displayed asynchronous wing supinations and hamations; the former wing movements were accompanied by swaying and abdominal flexures. Males also displayed synchronous supinations during courtship (Headrick and Goeden 1994).

*Courtship*: Males displayed abdominal pleural distensions (Fig. 6E) along with synchronous wing supinations and oriented toward females in petri dish arenas during courtship displays. If females remained still, mountings were attempted, but females usually were aggressive toward males and lunged at them with their wings spread open. Only two successful mountings were observed. In both, a male jumped onto the dorsum of a female from behind; she responded by pushing vigorously at him with her hind legs. The male grasped the female with his front legs on top of her abdomen near her thorax, while his middle

legs wrapped around the middle of her abdomen and his hind legs pulled upward on her oviscape.

*Copulatory induction behavior (CIB)*: The mounted male held the oviscape of the female upward with his hind legs and drummed his epandrium against its apex. He also rubbed his front legs asynchronously in 1 sec bursts against her abdominal terga. The male of one pair engaged in CIB for more than 10 sec, then dismounted without having successfully gained intromission. The male of a second pair engaged in CIB for ca. 10 sec, when the female exserted her aculeus and intromission was gained.

*Copulation*: Both adults of the pair that copulated remained quiet for ca. 5 min until the male extended his wings, turned, and stepped down from the female, and walked away while pulling his aedeagus from her aculeus.

*Field observations*: Females of *T. actinobola* were examined on preblossom and flowering *A. sphaerocephalus* at Snow Creek on 31.iii.1992 and at the mouth of Oriflamme Canyon on 9.iv.1992. No males of *T. actinobola* were observed, as presumably they had mated and died by then.

*Daily activity and abundance*: By 10:00 h, *T. actinobola* females began to appear on *A. sphaerocephalus* plants at Snow Creek and up to 12 *T. actinobola* females were observed per plant throughout the day ($n = 10$). The females were actively, rapidly walking, exploring immature flower heads, probing, and displaying asynchronous wing supinations during these activities.

*Oviposition*: Females touched the ovipositor apex to the side of small flower heads, ca. 1–4 mm diam ($n = 3$). The apex was traced along the edges of bracts attempting to locate a site to gain purchase for penetration. Females faced away from the center of flower heads during oviposition and curled their ovipositor beneath their bodies. The aculeus tip was inserted into the flower head, after which they paused for ca. 2 min. After oviposition the aculeus was retracted and fe-

males walked upon the flower head, or flew to another head.

Seasonal history.—The life cycle of *T. actinobola* in southern California follows an aggregative pattern in which the long-lived adults in reproductive diapause overwinter and aggregate to mate on preblossom host plants in the spring (March–April) (Headrick and Goeden 1994). They reproduce at first on *Acamptopappus* spp. in the Colorado Desert, then on this genus and *Amphipappus fremontii* in the higher-elevation Mojave Desert (Munz 1974, Hickman 1993). A second generation is produced each year on *Gutierrezia* spp. The larger form of *T. actinobola* also is bivoltine on its annually or biannually flowering host plants in southern California.

Natural enemies.—Four species of chalcidoid Hymenoptera were reared from individual puparia and mature flower heads of *A. sphaerocephalus* bearing puparia of *T. actinobola* as solitary, primary, larval-pupal endoparasitoids: *Eurytoma veronia* Bugbee (Eurytomidae), *Halticoptera* sp. (Pteromalidae), *Mesopolobus* sp. (Pteromalidae), *Pteromalus* sp. (Pteromalidae).

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